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# *HADOCERAS TAYLORI,* A NEW GENUS AND SPECIES OF PHREATIC HYDROBIIDAE (GASTROPODA: RISSOACEA) FROM SOUTH-CENTRAL TEXAS

Robert Hershler and Glenn Longley

*Abstract.*—*Hadoceras taylori,* a new genus and species of Hydrobiidae, Littoridininae, is described from three localities in Real County, Texas. This phreatic species may well range throughout the southern portion of the Edwards Plateau and into northern Mexico. The detailed morphological description provided for this species includes aspects of the shell, operculum, pallial cavity, digestive system, and reproductive system of both sexes. Generic separation of *Hadoceras* from similar-shelled late Tertiary *Orygoceras* is warranted by both morphological and ecological considerations. A suite of unique characters, including the uncoiled, horn-like shell and concentric operculum with ventral process, separates *Hadoceras* from other known phreatic littoridinines of south-central Texas and northern Mexico.

Taylor's (1974) discovery of living phreatic snails from Roaring Springs, Texas referable to *Orygoceras* Brusina, 1882, a genus previously known only as late Tertiary fossils from Idaho and southeastern Europe, ranks as a particularly exciting event in the recent history of freshwater malacology. The uncoiled, horn-like shell of *Orygoceras* is highly unusual among gastropods (Rex and Boss 1976) and the systematic placement of this genus has long been debated (Taylor 1974). Taylor (1974) concluded that living *Orygoceras* is a hydrobiid (Prosobranchia: Rissoacea), but did not describe this species. His morphological study was necessarily limited as he collected a single live specimen, and various aspects of anatomy, including details of the male and female reproductive system critical to the systematic assessment of rissoacean snails, were not dealt with.

As part of an ongoing survey and systematic study of phreatic gastropods of south-central Texas (see Hershler and Longley, 1986) we collected more than 20 live *Orygoceras* sp. (including a number of adults) from Roaring Springs and two other springs in Real County, Texas. We describe this snail as *Hadoceras taylori,* a new genus and species of Hydrobiidae; provide a detailed morphological description of this taxon, including aspects of the male and female reproductive systems; and discuss the systematic relationships of *Hadoceras,* emphasizing comparisons with other members of the diverse phreatic hydrobiid fauna of south-central Texas and northern Mexico.

*Localities.*—*Hadoceras taylori* was collected during May 22–24, 1985 from the following three springs (see Fig. 1): a) Roaring Springs (unnamed on USGS topographic sheets), about 7.6 miles W of Camp Wood (water temperature 21.0°; conductivity 319.2 ymHOS; 5/23); b) Unnamed spring in South Prong Canyon, 6.6 miles W of Camp Wood (temperature 21.0°; conductivity 415.0 ymHOS; 5/23); and c) Unnamed spring at Jo Jan Van Camp, 9 miles N of Vance. All three springs are moderate-sized rheocrenes, with numerous orifices. They occur in the Nueces River drainage in the region where the southern edge of the Edwards Pla-

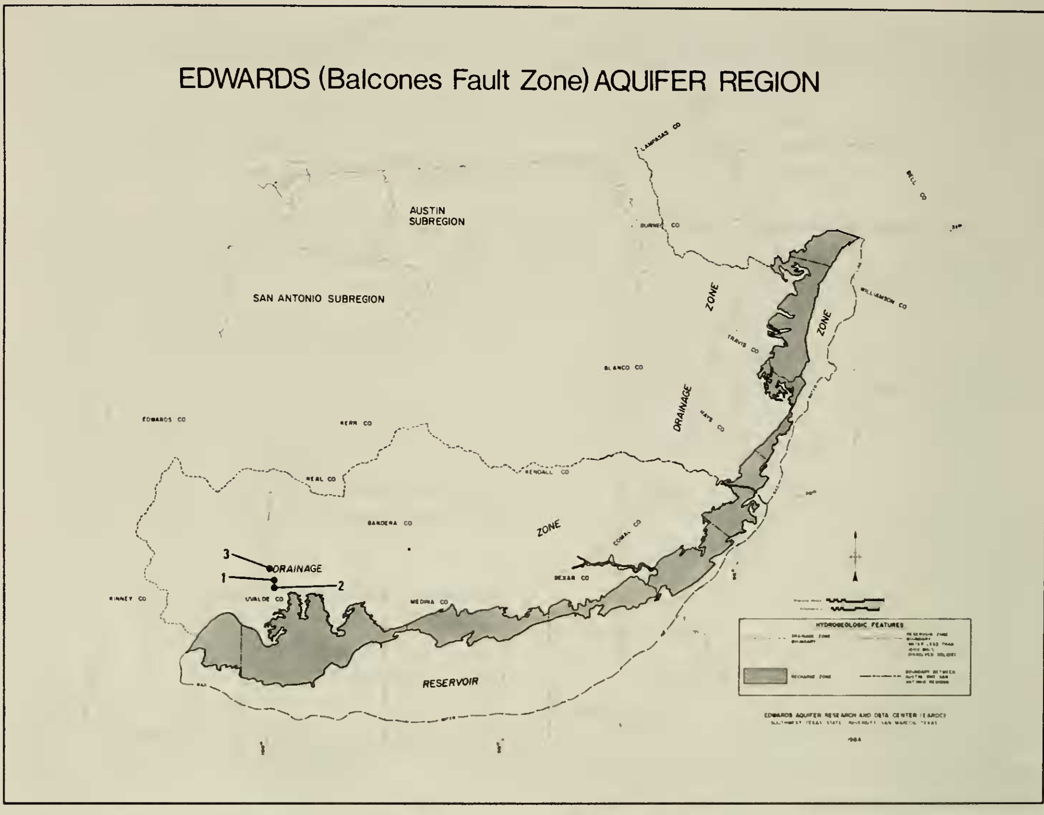



Fig. 1. Map of the Edwards (Balcones Fault Zone) Aquifer Region showing the three localities from which *Hadoceras taylori* were collected. The localities are Roaring Springs (1), an unnamed spring in South Prong Canyon (2), and an unnamed spring at Jo Jan Van Camp (3).

teau gives rise to the well-dissected Hill Country. The water-bearing unit feeding the springs is probably the Trinity group of lower Cretaceous limestone (Ashworth 1983).

*Methods.*—Three methods were used to collect *H. taylori* and other phreatic organisms at these localities. Sections of PVC pipe capped with fine (64 $\mu$) mesh netting at one end were placed overnight in spring orifices to filter the water stream emerging from underground. Cotton gauze was placed overnight in the orifices to serve as an artificial colonization substrate for these organisms. Finally, sediments in the uppermost sections of the spring runs were sifted using a fine hand sieve.

Methods of morphological study are those of Hershler and Longley (1986). Usage of body surface references follows that of Fretter and Graham (1962). All morphological data presented are from individuals collected from Roaring Springs. Unless otherwise indicated, unrelaxed preserved specimens (initially fixed in formalin) were used for anatomical study. A total of six individuals was dissected.

Family Hydrobiidae
Subfamily Littoridininae
*Hadoceras*, new genus

*Orygoceras* Brusina, 1882 (in part):33.

*Diagnosis.*—Shell (Figs. 2–4) minute (maximum dimension, less than 2.8 mm),

Fig. 2. Holotype (USNM 849000) of *Hadoceras taylori* (shell width, 2.37 mm).

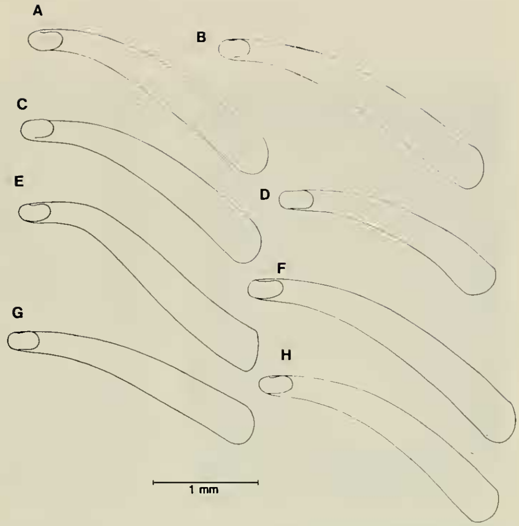
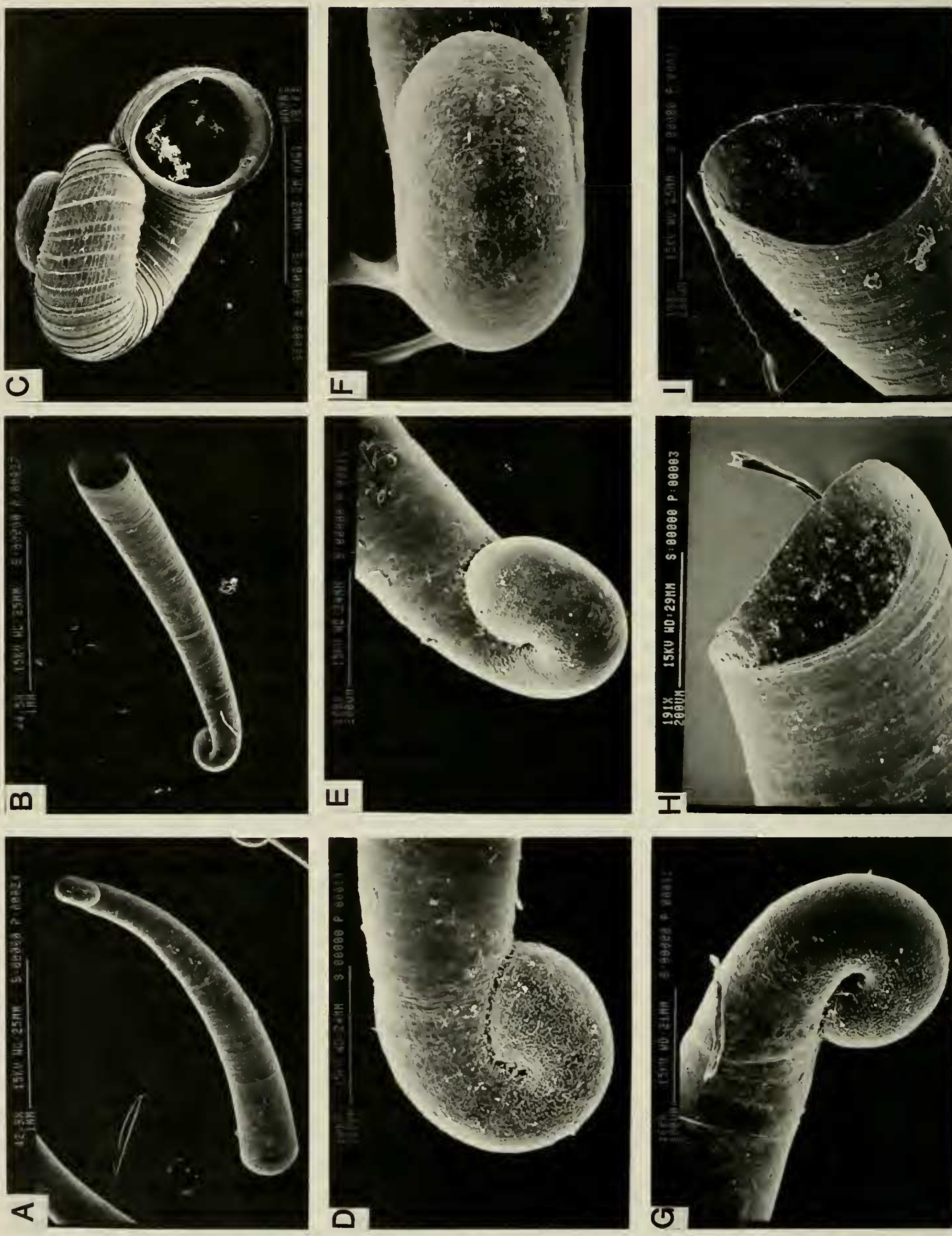



Fig. 3. Camera lucida drawings of shell outlines of *H. taylori,* including the holotype (A) and paratypes (D–H, USNM 849001). Note the variation in translation rate along the coiling axis.

colorless, transparent, horn-like in shape with uncoiled teleoconch and simple aperture (Fig. 4B, H, I). Protoconch with pitted microsculpture (Fig. 4D), teleoconch with strong collabral growth lines (Fig. 4H). Operculum (Fig. 5) concentric, with a large, peg-like, non-calcareous process on ventral surface. Animal unpigmented and without eyespots (Figs. 6, 7). Ctenidium absent (Fig. 7). Intestine (In) with loop on right side of style sac (Fig. 10) and coil in roof of pallial cavity (Figs. 6, 7). Central tooth of radula trapezoidal in shape, with a single pair of basal cusps arising from lateral angles (Figs. 8, 9). Pallial gonoducts (Pr, Ag, Fig. 6) displaced ventrally. Gonads consisting of non-lobed mass, occupying 20–25% of total body length. Pallial portion of prostate less than 20% of prostate length; anterior vas deferens exiting from anterior tip of prostate (Fig. 10C). Penis simple, without lobes or specialized glands (Fig. 10B). Capsule gland (Cg) with two tissue sections and terminal opening (Cga, Fig. 11). Albumen gland (Ag) loops posteriorly (around bursa (Bu)), with posterior tip joining oviduct (Ov, Fig. 11); sperm duct (Sdu) issuing from this juncture and connecting with anterior portion of spermathecal duct (Sd). Seminal receptacle absent; spermathecal duct and capsule gland opening jointly (Cga).

*Remarks.*—The morphological groundplan of *Hadoceras* clearly indicates that it is a member of the Hydrobiidae (see family definition in Davis 1979) and the presence of a spermathecal duct suggests placement in the Littoridininae (see Davis et al. 1982; Hershler 1985). Apart from its shell form, unique among hydrobiids, character-states distinguishing *Hadoceras* from other littoridinines include the concentric operculum with ventral process, unusual ventral displacement of the pallial gonoducts, and combination of minute adult size and simple penis.

There is little doubt that European *Orygoceras,* which has been considered as either an uncoiled valvatid or planorbid (Wenz 1938–44; Papp 1962), is distinct from *Hadoceras.* The shells of the former are not only much larger (to 10 mm) than those of *Hadoceras,* but also differ in form, having a much larger whorl expansion rate, non-circular aperture, and (often) macrosculptural de-


A
B
C
D
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velopment. The inferred habitat of European fossil *Orygoceras* is lacustrine (Taylor 1974), as opposed to the phreatic habitat of *Hadoceras*. A similar set of arguments suggests generic distinction of *Hadoceras* from the Idaho fossil *Orygoceras*, which are as large as those from Europe, and are similarly found in ancient lake bed deposits (Dall 1924; Yen 1944; Taylor 1966).

*Type species.*—*Hadoceras taylori* (by original designation).

*Etymology.*—From the Greek words *Hades* and *keras*, meaning the god of the underworld and a horn, respectively, and referring to the subterranean habitat and horn-like shell of this genus. Gender neuter.

*Distribution.*—*Hadoceras taylori* occurs in phreatic habitats associated with Cretaceous limestone aquifers in Real County, Texas. Davis (1983) reports fresh shells referable to this species from Williamson County, and it is likely that the species ranges throughout limestone aquifers in the southern edge of the Edwards Plateau. In addition, live specimens of what appears to be the same species were collected by the senior author from groundwater outlets in the Cuatro Cienegas Basin, northeastern Mexico (Hershler 1985). Fossil shells in the 2–3 millimeter range representing possibly a second *Hadoceras* sp. were collected by W. Pratt from an archaeological site in the Las Vegas Wash (Nevada) northeast of Henderson. The shells were radiocarbon dated as 400 years B.P. and the inferred fossil habitat at the site is a marshy spring area (W. Pratt, pers. comm. 1985).

*Habitat.*—The collection of living *H. taylori* by placing nets into groundwater outlets, nets that cannot be entered by crenobiontic organisms, demonstrates that this species does occur in the phreatic environment. It is also apparent from collections taken from the upper spring runs that the species also inhabits this epigean habitat. We do not concur with the assertions of Taylor (1974) and Davis (1983) that *H. taylori* is necessarily interstitial in habit. The Cretaceous limestone aquifers in south-central Texas are extremely porous, with openings ranging upwards in size to large caverns (Brune 1975), and there is no reason to suspect that the species is limited to interstitial habitats. The presence of much larger phreatic organisms in these aquifers, including vertebrates, attests to the use of non-interstitial habitats (Longley 1981).

*Associated fauna.*—Phreatic organisms collected with *H. taylori* include another phreatic hydrobiid, *Phreatodrobia* sp. (Fig. 4C), as well as diverse crustaceans, including isopods, amphipods, and copepods.

### *Hadoceras taylori*, new species
Figs. 1–12

*Orygoceras* sp. Taylor, 1974:93.

*Description.*—Shell: For 8 (fresh) adult shells, height and width ranged from 0.946–1.81 and 2.00–2.03 mm respectively (Table 1). The thin shell is transparent when fresh, but has an opaque, white aspect in older specimens. The protoconch has 1.0–1.12 whorls, a diameter of about 0.32 mm, and coils in the same plane as the beginning of the teleoconch (Fig. 4A, F). The junction between the protoconch and teleoconch is quite noticeable (Fig. 4D), often due to a sudden increase in diameter of the generating curve, or sudden change in direction of coiling at the beginning of the teleoconch. The teleoconch typically gently curves away from and down the coiling axis with only a slight whorl expansion, producing the horn-

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Fig. 4. Scanning electron micrographs of shells of *H. taylori* (A, B, D–I) and *Phreatodrobia* sp. (C). The protoconch is shown from above (D), below (G), and from the side (F, 300×). The aperture is shown from above (H, inner lip to the right) and below (I, inner lip above).

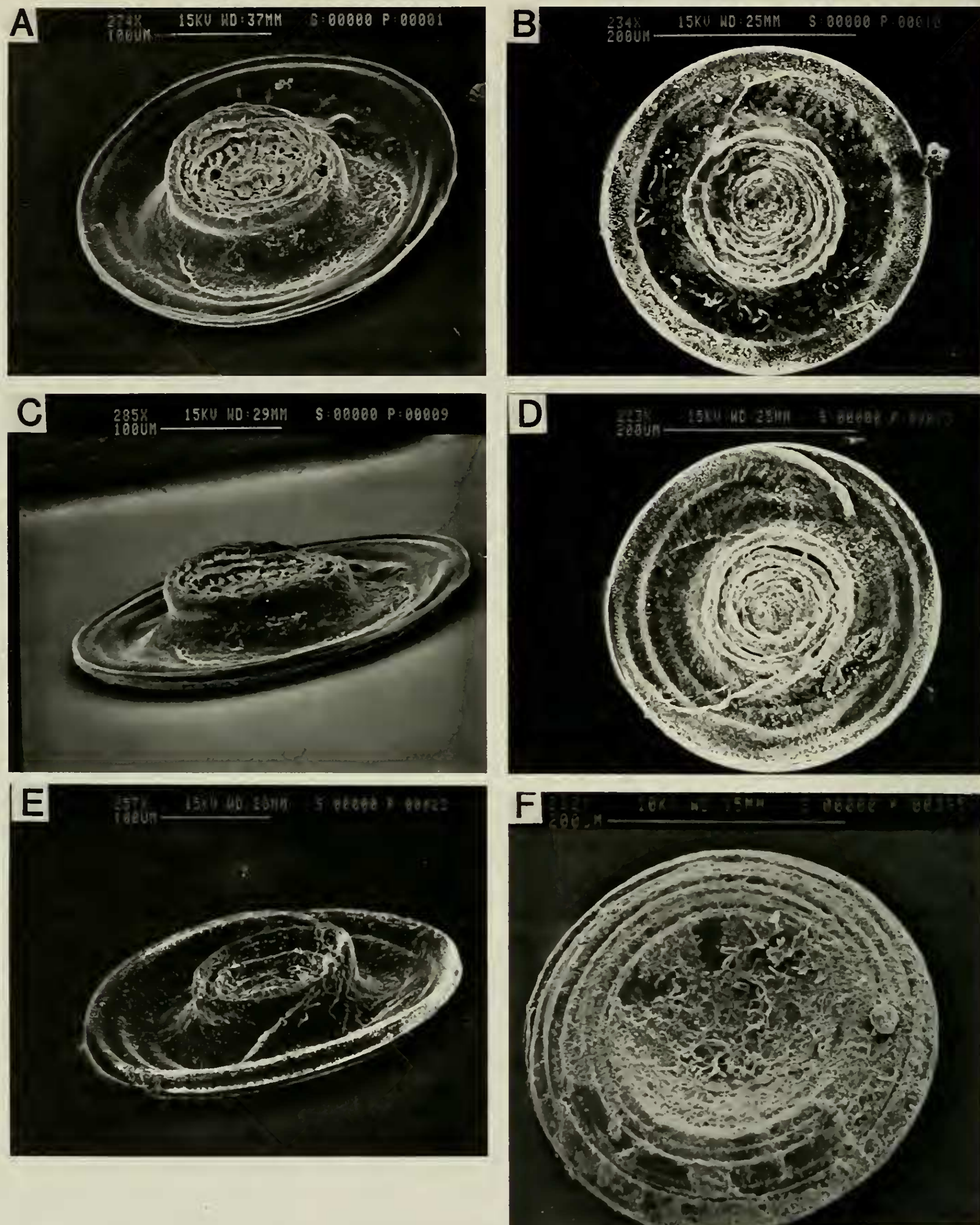


Fig. 5. Scanning electron micrographs of the operculum of *H. taylori* showing the ventral (A–E) and dorsal (F) aspects.

like shell shape, but the rate and nature of whorl translation vary, as seen in Fig. 3 and reflected in the above data. Note that the teleoconch may initially translate slightly above the protoconch, or suddenly dip down the coiling axis. The teleoconch does not coil in a single plane, but is somewhat bowed (towards the viewer in Fig. 3). The aperture, while near-circular (diameter of 0.35 mm), does not lie in a single plane as the inner lip is rather advanced. While not noticeably flared, the aperture is sometimes slightly expanded at the outer lip (Fig. 4H). The teleoconch growth lines are especially pronounced at the aperture.

*Operculum.*—The horny operculum is near-circular (Fig. 5B, D, F), with a typical diameter of 0.31 mm. The ventral process, centrally located, occupies a good portion of the operculum area. When viewed dorsally, this central region appears depressed (Fig. 5F). The portion of the operculum peripheral to the ventral process is also thickened and somewhat curved in the ventral direction (Fig. 5C, E). Of the 7–8 operculum whorls, which are arranged in near-concentric circles, the earliest 4 are located in the area occupied by the ventral process. Note that the distal end of the ventral process is concave, reflecting the progressive increase in process height from the first to fourth whorl. After the fourth whorl the process height then quickly decreases to the level of the peripheral portion of the operculum.

*General anatomy.*—A set of anatomical data obtained from each of 4 specimens (2 males, 2 females) is given in Table 2. While lacking melanin pigment, the body of the snail does have black, spherical granules typically concentrated in 3 areas: on the right side of the digestive gland, where it covers the stomach and ventral to the gonad (Fig. 6A); and on the left side of the style sac (not figured). Apart from the red-pink color seen in the buccal mass and foot (due to hemoglobin), yellow-green color of the prostate (Pr), and yellow color of the ovary (Ova),

Table 1.—Shell height and width (mm) for the eight adult specimens of *Hadoceras taylori* shown in Fig. 4.

| | Shell height | Shell width |
|---|---|---|
| Holotype | 1.20 | 2.37 |
| Paratype | 1.82 | 2.15 |
| Paratype | 1.12 | 2.00 |
| Paratype | 0.95 | 2.44 |
| Paratype | 1.81 | 2.41 |
| Paratype | 1.34 | 2.17 |
| – | 1.20 | 2.63 |
| – | 1.27 | 2.06 |

the only other color visible in the animals is in the stomach, style sac and intestine, where the food contents and faecal pellets appear brown.

The illustration of the head in Fig. 7 is based on examination of a single, somewhat damaged live specimen in a partly contracted state. In a more typical live individual the snout (Sn) is probably less squat and the tentacles (Tn) more elongate, as illustrated by Taylor (1974, fig. 1). Terminal setae on the tentacles, figured by Taylor (1974, fig. 1), were not visible in the contracted specimens examined. The inner base of the tentacles has a dense concentration of clear, crystalline granules (Fig. 7).

As seen in Fig. 6, the pallial gonoducts (Pr, Ag) are situated more ventrally than is typical of hydrobiids (and prosobranchs in general), and actually lie over the oesophagus. The functional necessity for such a shift may be the need to accommodate the large kidney and intestinal loop on the style sac that lie dorsal to the gonoducts. This space constraint is also reflected in the unusual narrow nature of both gonoducts.

*Pallial cavity.*—The contents of the pallial cavity, which occupies 21–26% of the total body length, are shown in Fig. 7. While no trace of the ctenidium is seen, the large osphradium (Os), occupying 27–34% of the pallial cavity length, is found in its usual position. The intestine (In) makes a large, U-shaped loop that fills much of the pos-

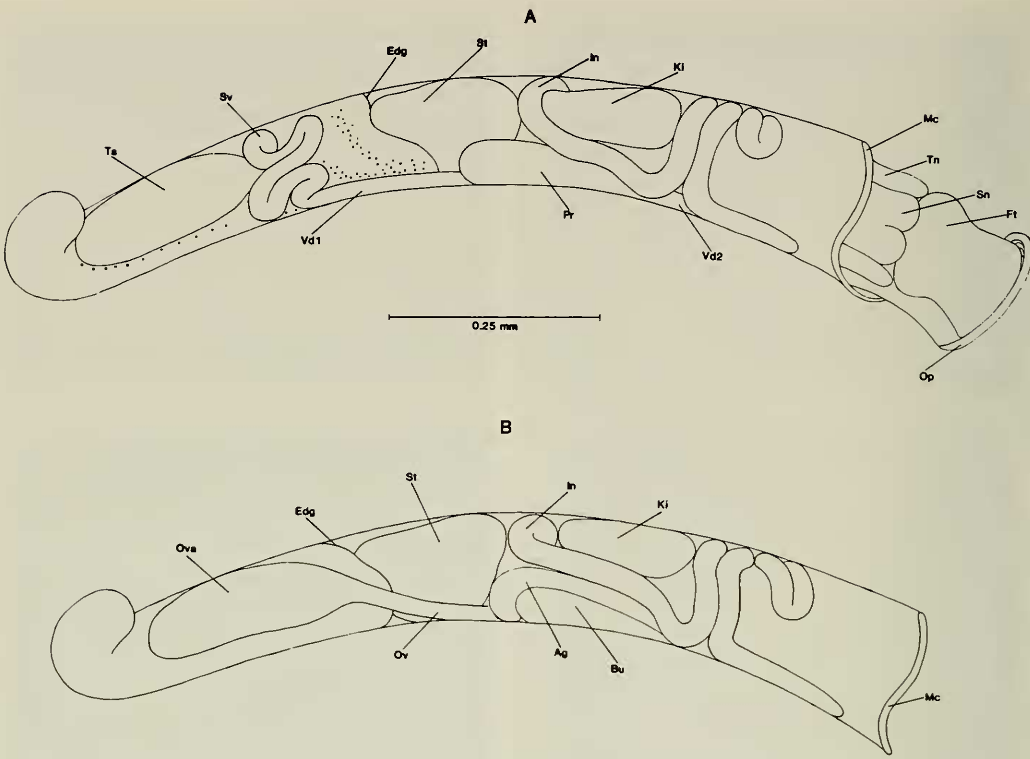


Fig. 6. Male (A) and female (B, minus the head/foot) *H. taylori,* viewed from the right lateral aspect. Ag, albumen gland; Bu, bursa copulatrix; Edg, anterior end of the digestive gland; Ft, foot; In, intestine; Ki, kidney; Mc, mantle collar; Op, operculum; Ov, oviduct; Ova, ovary; Pr, prostate; St, stomach; Sv, seminal vesicle; Tn, tentacle; Ts, testis; Vd1, posterior vas deferens; Vd2, anterior vans deferens.

terior portion of the pallial cavity roof, the loop actually bending back upon itself when the pallial cavity roof is viewed in its normal curved orientation (Fig. 6), and not flattened out as in Fig. 7. The anus is situated within 0.06 mm of the mantle edge. The pericardium (Pc) is rather small and narrow, whereas the kidney (Ki) is enlarged, with a simple, non-fleshy opening.

*Digestive system.*—The radula of *H. taylori* is shown in Figs. 8 and 9. The generalized cusp formulae, based on examination of scanning electron microscope photographs of 4 radulae, are as follows: central, 4(5)-1-4(5)/1-1; lateral, (4–6)-1-5; inner marginal, 17–21; outer marginal, 15–16. The width of the central tooth is about 0.0097 mm. Note that the central cusps of the central and lateral teeth are enlarged relative to other cusps on these teeth. Also note the relatively large basal cusps on the central teeth and the well-excavated basal process. The shape of the cusps on the central teeth varies from hoe-like (Fig. 8B) to dagger-like (Fig. 8D).

The oesophagus (Oes) coils once immediately upon exiting from the head/foot mass (Fig. 7). The two stomach chambers (Ast, Pst) are poorly differentiated externally (Fig. 10A) and there is no caecal appendix. Two solid masses of digestive gland exit from the single opening of the stomach (Odg). The digestive gland lacks noticeable tubular swellings. The stomach is typically only slightly longer than the narrow style sac (Sts). Note that the intestine (In) exits from the left side of the style sac very close to where the latter joins the stomach.

*Male reproductive morphology.*—The seminal vesicle (Sv) exits from the anterior tip of the testis and consists of a tight mass of several coils, measuring about 0.2 by 0.2 mm, that fills the space between the testis and stomach. The prostate (Pr), which is 5 times as long as wide, overlies a portion of the anterior stomach chamber. Note that the vas deferens (Vd1) enters the prostate near its mid-line, which is considerably posterior to the end of the pallial cavity (Fig. 10C). The anterior vas deferens (Vd2) exits from the tip of the prostate as a thickened tube, which then travels 0.6–0.7 mm anteriorly in the pallial cavity roof before turning back posteriorly to enter the "neck" and travel a similar distance to the base of the penis (Pn, Fig. 7).

The penis (Fig. 10B) coils counter-clockwise in a tight fashion, on the "neck" behind the snout. While lobes are absent, both edges of the penis have small folds, although the folds end on the inner edge at two-thirds of the penis length from the base. The vas deferens does not coil greatly in the penis and is eversible at the penis tip. The single penis examined from a living individual (shown in Fig. 10B) lacked cilia, although columnar epithelia were seen along both edges. Single large spherical granules occur along the proximal two-thirds of the penis.

*Female reproductive morphology.*—Large, spherical oocytes were seen in the posterior portion of the ovary of several specimens. Note that the anterior end of the ovary (Ova) abuts the posterior end of the stomach (St, Fig. 6B). The oviduct (Ov) exits from the anterior end of the ovary and disappears to the left side of the bursa and pallial oviduct (Bu, Ag, Fig. 6B).

The pallial oviduct (Cg + Ag, Fig. 11) is unusually narrow along its entire length. The anterior section of the capsule gland is twice as long (but much narrower) as the posterior section, and clear rather than white. The

Table 2.—Measurements (mm) of organs and structures for four specimens of *Hadoceras taylori.* M = male, F = female.

| Specimen | 1 (M) | 2 (M) | 3 (F) | 4 (F) |
|---|---|---|---|---|
| Shell width | 2.54 | 2.51 | 2.51 | 2.57 |
| Body length | 2.04 | 1.92 | 1.96 | 2.26 |
| Snout length | 0.16 | 0.14 | 0.18 | 0.12 |
| Tentacle length | 0.16 | 0.14 | 0.18 | 0.14 |
| Pallial cavity length | 0.42 | 0.41 | 0.51 | 0.59 |
| Osphradium length | 0.14 | 0.14 | 0.14 | 0.16 |
| Osphradium width | 0.089 | 0.079 | 0.10 | 0.12 |
| Stomach length | 0.36 | 0.34 | 0.34 | 0.36 |
| Stomach width | 0.22 | 0.22 | 0.22 | 0.24 |
| Style sac length | 0.30 | 0.20 | 0.28 | 0.32 |
| Style sac width | 0.10 | 0.10 | 0.11 | 0.10 |
| Gonad length | 0.44 | 0.38 | 0.50 | 0.51 |
| Gonad width | 0.16 | 0.16 | 0.14 | 0.20 |
| Prostate length | 0.50 | 0.50 | — | — |
| Prostate width | 0.10 | 0.12 | — | — |
| Pallial prostate length | 0.10 | 0.08 | — | — |
| Penis length | 0.20 | 0.18 | — | — |
| Pallial oviduct length | — | — | 0.87 | 0.83 |
| Pallial oviduct width | — | — | 0.18 | 0.10 |
| Bursa length | — | — | 0.42 | 0.59 |
| Bursa width | — | — | 0.12 | 0.14 |

albumen gland, which is thin, clear, tubular, and decidedly non-glandular; extends posteriorly to slightly overlap the stomach, and then loops anteriorly with its length slightly overlapping the right side of the bursa (Bu, Figs. 10B, 11). Although egg capsules were not found, we suspect that the species is oviparous and not ovoviviparous.

The oviduct (Ov) has a single, swollen coil on the left side of the bursa. The coil has a pink sheen and is the probable site of sperm storage, given the absence of a seminal receptacle. Just anterior to this coiled section, the oviduct opens into the albumen gland, the connection being difficult to recognize as the terminal portion of the albumen gland is extremely fragile and easily ruptured. The sperm duct (Sdu) issuing from this point is very narrow relative to the coiled oviduct, and extends anteriorly, looping back to the right side of the spermathecal duct (Sd) to enter the pallial cavity roof and finally join

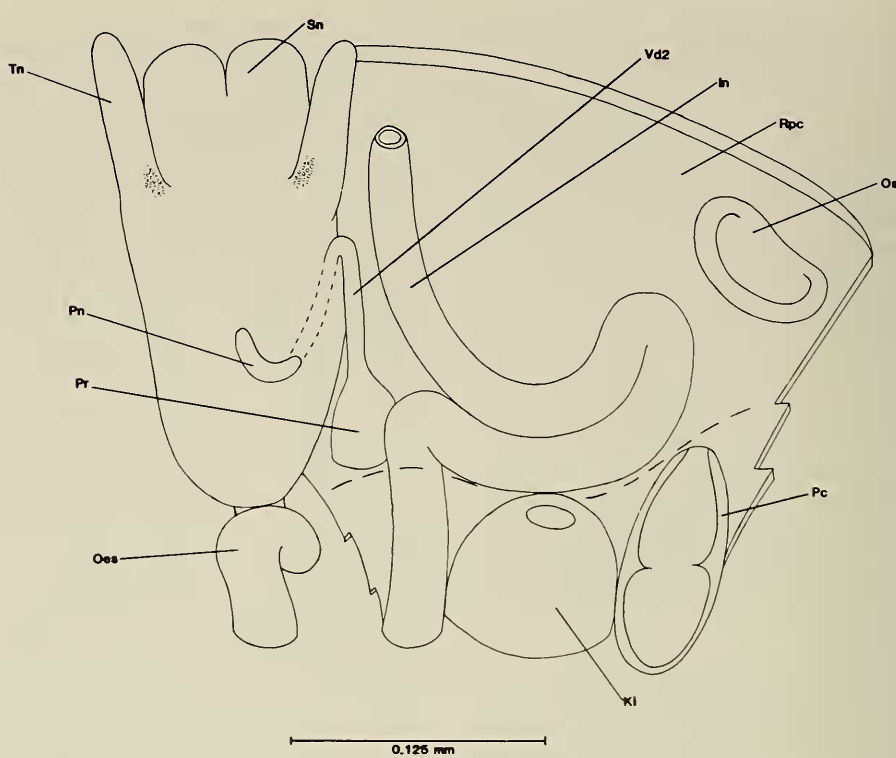


Fig. 7. Head and contents of the pallial cavity of *H. taylori.* The length of the pallial cavity roof has been cut along the extreme left side and then flattened out to the right. The dashed line indicates the posterior end of the pallial cavity. The posterior portion of the prostate has been removed. In, intestine; Ki, kidney; Oes, oesophagus; Os, osphradium; Pc, pericardium; Pn, penial attachment area; Pr, prostate, Rpc, roof of pallial cavity; Sn, snout; Tn, tentacle; Vd2, anterior vas deferens.

the spermathecal duct (Osdu) in the anterior portion of the pallial cavity. The bursa (Bu) is white and very solid (compared to the pallial oviduct). While the main body of the bursa is pear-shaped, it narrows anteriorly and then swells to form a vestibule (just anterior to the end of the pallial cavity), which then gives rise to the narrower spermathecal duct. The spermathecal duct is tightly appressed to the capsule gland, and the wide common opening of the two (Cga) is located anterior to the anus and close to the mantle edge.

*Holotype.*—USNM 849000 (Figs. 2, 3A).

*Paratypes.*—USNM 849001 (Figs. 3D–H), UF 67466.

*Type locality.*—Roaring Springs, Real County, Texas.

*Etymology.*—Named after Dwight W. Taylor, in recognition for his discovery of this species and immense contributions to the study of western American freshwater molluscs.

## Systematic Relationships among Phreatic Littoridinines

With the description of *H. taylori* the known phreatic littoridinine fauna of south-central Texas and northeastern Mexico totals five genera and six species. A comparison between *Hadoceras* and the other four genera, involving 21 characters, is given in

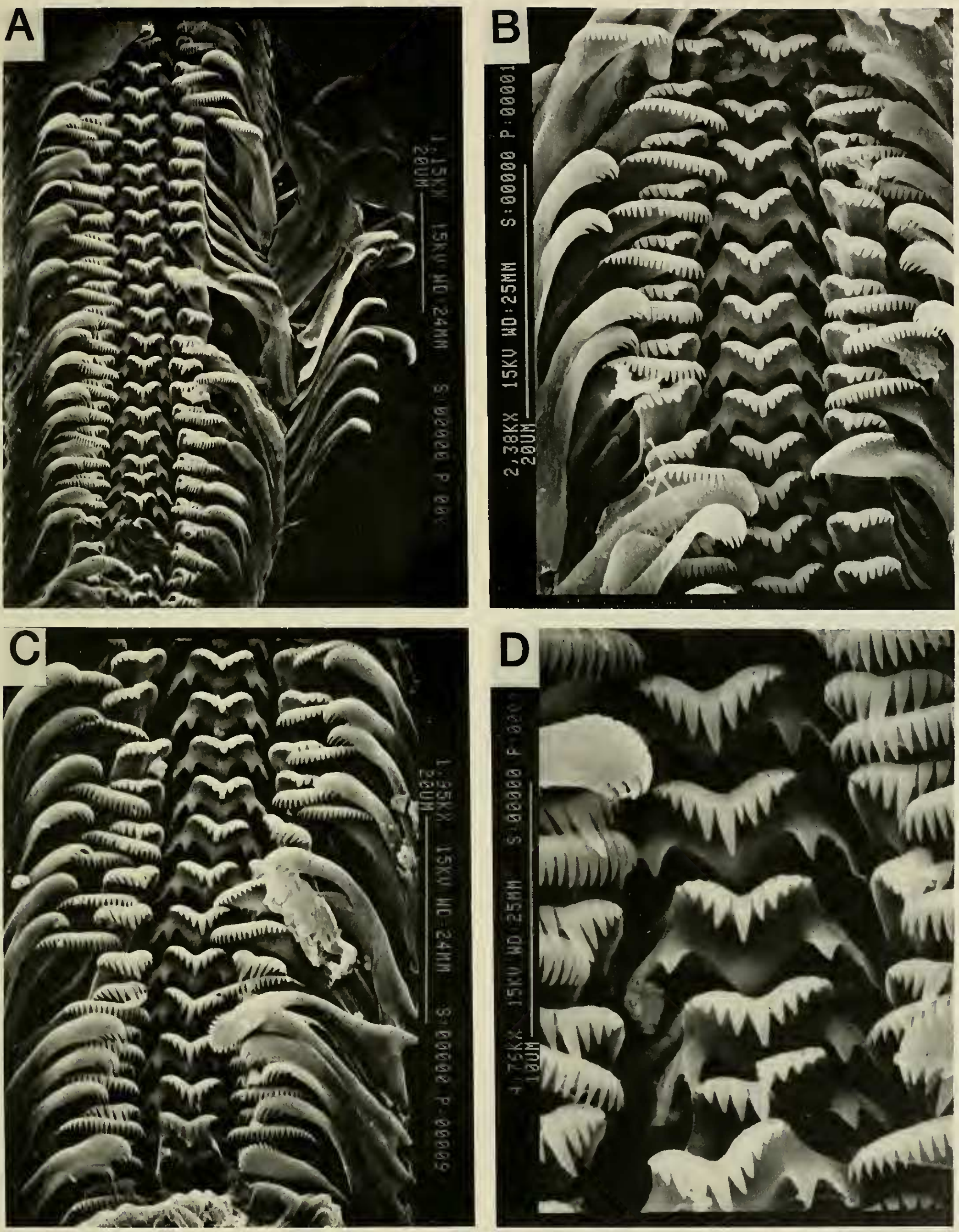


Fig. 8. Scanning electron micrographs of radulae of *H. taylori.* A–C, Sections of the radular ribbon; D, Close-up of central teeth.

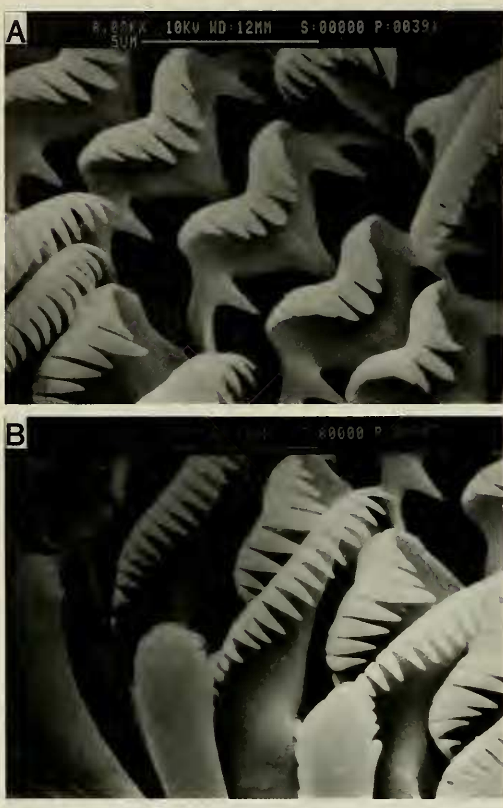


Fig. 9. Scanning electron micrographs of radulae of *H. taylori.* A, Close-up of central teeth; B, Close-up of lateral, inner marginal and outer marginal teeth.

Table 3. A phenogram, based on simple averaging of percent differences among generic pairs, is shown in Fig. 12.

The most similar pair, linking at 33% difference, are *Paludiscala* and *Coahuilix,* both endemic to the Cuatro Cienegas Basin, Mexico. The similarity between these genera extends to details of the anterior portion of the female reproductive system, with both taxa having a large-sized bursa (but no seminal receptacle) ventral to the pallial oviduct, and a sperm duct travelling from the right side of the bursa to enter the posterior portion of the albumen gland. While differing in features involving shell form (*Coahuilix,* planispiral; *Paludiscala,* elongate-conic), nature of the openings of the spermathecal duct and capsule gland (separate vs. fused), and site of sperm storage (albumen gland proper vs. albumen gland pouch), the two taxa are probably part of the same local radiation and perhaps should even be considered congeneric. *Stygopyrgus* and *Balconorbis,* both occurring in the Edwards (Balcones Fault Zone) Aquifer in south-central Texas, link at 48% difference and have rather dissimilar groundplans of the anterior portion of the female reproductive system. We have speculated (Hershler and Longley 1986) that *Balconorbis* may belong to the *Paludiscala-Coahuilix* group, despite differences in characters such as protoconch microsculpture type, as its arrangement of the anterior portion of the female reproductive system is derivable (involving loss of the bursa) from that of the latter group. In *Stygopyrgus* the oviduct loops on the left side of the albumen gland, and enters the anterior end of this gland, with the spermathecal duct arising from this juncture and then receiving the duct of the seminal receptacle well into the pallial cavity. This unique arrangement, coupled with the mammiform penial glands seen in this genus (versus bulbous apocrine glands in the above three genera), suggests that *Stygopyrgus* belongs to a second radiation of phreatic littoridinines.

*Hadoceras* differs from the other four genera by 57–68% of the characters considered and has a number of unique character-states, including the horn-like shell, concentric operculum with ventral process, intestinal loop on the right side of style sac, lack of penial lobes, and ventral displacement of the pallial gonoducts. The anterior portion of its female reproductive system does not closely resemble the arrangements seen in either of the other genera considered: note the unusual nature of the albumen gland, which is slender, non-glandular, and loops around the periphery of the bursa, and the elongate sperm duct, which joins the spermathecal duct well into the pallial cavity. Given the diversity of unique character-states seen in *Hadoceras,* we conclude that

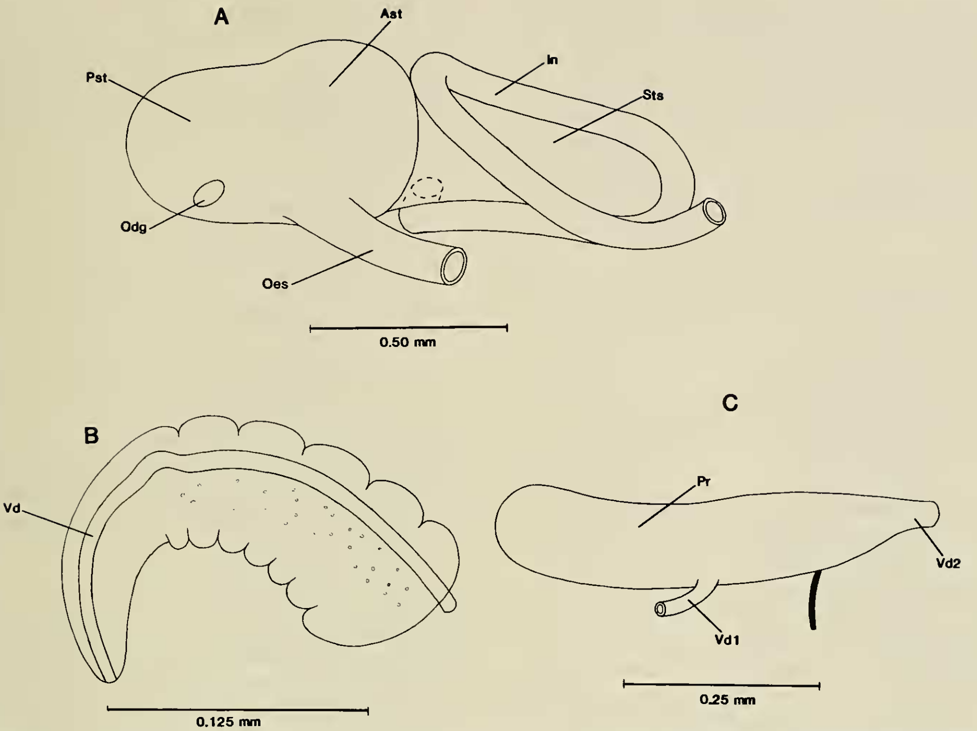


Fig. 10. Stomach (A), penis (B), and prostate (C) of *H. taylori.* The right aspect is shown in A and B, and the ventro-right lateral aspect shown in C. The dark, curving line in C indicates the posterior end of the pallial cavity. Ast, anterior stomach chamber; In, intestine; Odg, opening of digestive gland; Oes, oesophagus; Pr, prostate; Pst, posterior stomach chamber; Sts, style sac; Vd, vas deferens; Vd1, posterior vas deferens; Vd2, anterior vas deferens.

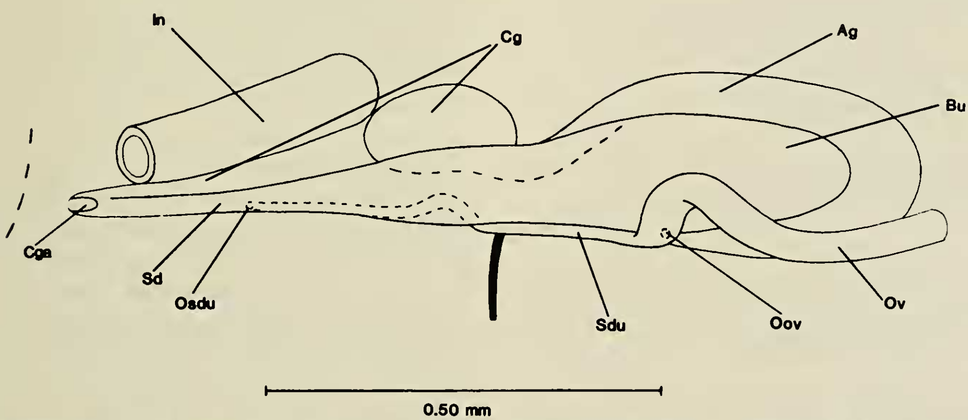


Fig. 11. Left lateral aspect of the anterior portion of the female reproductive system. The posterior portion of the intestine (In) has been removed. The thick curving line indicates the posterior end of the pallial cavity while the dashed line (to the left) indicates the mantle edge. Ag, albumen gland; Bu, bursa copulatrix; Cg, capsule gland; Cga, common opening of the capsule gland and spermathecal duct; In, intestine; Oov, opening of the oviduct into the albumen gland; Ov, oviduct; Osdu, opening of the sperm duct into the spermathecal duct; Sdu, sperm duct; Sd, spermathecal duct.

Table 3.—Comparison of phreatic littoridinine genera involving 21 characters. B = *Balconorbis*, S = *Stygopyrgus*, P = *Paludiscala*, C = *Coahuilix*, and H = *Hadoceras*. Data for genera other than *Hadoceras* are from Hershler (1985) and Hershler and Longley (1986).

| Character | Genus | | | | |
|---|---|---|---|---|---|
| | B | S | P | C | H |
| Shell | | | | | |
| 1. Maximum dimension >2.0 mm (0, 1) | 0 | 0 | 1 | 0 | 1 |
| 2. Shell form: a) planispiral (0) b) elongate-conic (1) c) horn-like (2) | 0 | 1 | 1 | 0 | 2 |
| 3. Protoconch microsculpture: a) spiral lines (0) b) punctate (1) | 0 | 1 | 1 | 1 | 1 |
| 4. Teleoconch sculpture: a) spiral lines (0) b) collabral costae (1) c) absent (2) | 0 | 0 | 1, 2 | 2 | 2 |
| Operculum | | | | | |
| 5. Operculum concentric (0, 1) | 0 | 0 | 0 | 0 | 1 |
| 6. Operculum with ventral process (0, 1) | 0 | 0 | 0 | 0 | 1 |
| Nonreproductive anatomy | | | | | |
| 7. Ctenidium present (0, 1) | 0 | 0 | 1 | 0, 1 | 0 |
| 8. Intestinal loop on style sac (0, 1) | 0 | 0 | 0 | 0 | 1 |
| 9. Intestinal loop in pallial cavity roof (0, 1) | 1 | 1 | 0 | 1 | 1 |
| Reproductive morphology | | | | | |
| 10. Pallial gonoducts displaced ventrally (0, 1) | 0 | 0 | 0 | 0 | 1 |
| 11. Number of penial lobes: a) 0 (0) b) 1 (1) c) 2 (2) | 1 | 2 | 1 | 1 | 0 |
| 12. Position of lobe(s): a) outer curvature of penis (0) b) inner curvature (1) | 0 | 1 | 0 | 0 | — |
| 13. Penial gland type: a) apocrine (0) b) mammiform (1) | 0 | 1 | 0 | 0 | — |
| 14. Anterior coil of oviduct: a) ventral to pallial oviduct (0) b) on left side of pallial oviduct (1) c) absent (2) | 0 | 1 | 2 | 2 | 1 |
| 15. Oviduct opens into: a) posterior tip of albumen gland (0) b) posterior section of albumen gland (1) c) anterior end of albumen gland (2) | 0 | 2 | 1 | 1 | 0 |
| 16. Albumen gland with posterior loop (0, 1) | 1 | 0 | 0 | 0 | 1 |
| 17. Bursa copulatrix present (0, 1) | 0 | 0 | 1 | 1 | 1 |
| 18. Seminal receptacle present (0, 1) | 0 | 1 | 0* | 0 | 0 |
| 19. Openings of spermathecal duct and capsule gland: a) fused (0) b) separate (1) | 0 | 0 | 0 | 1 | 0 |
| 20. Number of capsule gland tissue sections: a) 2 (0) b) 3 (1) | 0 | 0 | 1 | 0 | 0 |
| 21. Capsule gland opening muscularized (0, 1) | 0 | 1 | 0 | 1 | 0 |

* Secondarily-derived seminal receptacle present.

this genus represents yet another separate phreatic invasion within the Littoridininae. Epigean littoridinines having either a simple penis, or a penis having mammiform or apocrine glands are known from Texas and northern Mexico (see Hershler 1985) and represent possible ancestors of the three phreatic radiations mentioned above. Further study of the diverse epigean littoridine fauna of the region will be necessary, however, before the above phylogenetic speculations can be tested.

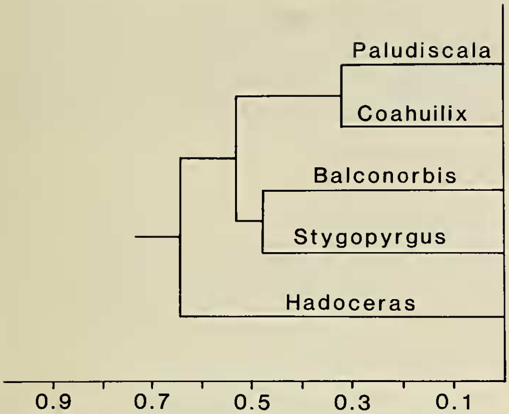


Fig. 12. Phenogram showing similarities among *Hadoceras* and other phreatic littoridinines from Texas and northeastern Mexico. Data used to generate the phenogram are given in Table 3.


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